

ANATOMY OF EQUISETUM GIGANTEUM

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(WITH SEVEN FIGURES)

I. Material

While studying the anatomy of the cone of *Equisetum giganteum* serial preparations were made of some of the upper nodes of the fertile branches. These branches are small and usually possess eleven ribs and bundles. They were collected in Chili by Professor R. C. McLEAN, who most kindly handed them over to me. Serial transverse sections have also been prepared from the upper part of a large young main stem of *E. giganteum* from the West Indies, for which I am indebted to Professor F. W. OLIVER. This series of sections extended from a level distinctly below one node to a point near the upper limit of the next node. The complete internode was about 1 cm. in length, and would doubtless have elongated much more. This stem had thirty-two bundles and ribs.

So far as I am aware, all accounts of the anatomy of *E. giganteum* since MILDE'S (11) in 1867, are based upon a short description by GWYNNE-VAUGHAN (7) that appeared in 1901. As my observations differ in some points from his, and in others supplement and confirm the details given by him, it seems advisable to publish a short account of the specimens studied.

II. Node of young main stem

Taking first the large young vegetative stem, the internode possesses a wide central cavity, about 6 mm. in diameter, the total diameter of the stem being about 7.75 mm. The bundles are oval in shape, with the longer axis directed radially, and each is surrounded by a separate endodermis.¹ The vallecular canals are about the size of the bundles and of much the same shape as these. Under each rib of the stem is a tooth of sclerenchymatous fibers,

¹ In none of the internodes examined was any trace observed of the common outer sheath of the bundles figured by MILDE (*pl. 21, fig. 4*).

projecting inward to within one to four cells of the endodermis surrounding the bundles.

The carinal canals are large, especially considering the youth of the specimen, and occupy about one-third of the bundle. The remains of one or two tracheids may adhere to the edges of the carinal canal, but all trace of the protoxylem has frequently disappeared over long stretches. The metaxylem forms two lateral, nearly parallel bands that converge slightly toward the periphery of the bundle. Usually each band consists of a single row of tracheids, although locally there are often two tracheids lying side by side. In any case the band of metaxylem is markedly narrower toward the periphery of the bundle, because the tracheids here are always much smaller. The tracheids, of which each band contains from seven to fifteen, usually about twelve, increase steadily in size toward the interior of the bundle. This "internodal" condition of the bundle, which in essentials is that characteristic of the whole genus, is shown diagrammatically in fig. 1, stage 1.

The node was slightly oblique, so that a section apparently nearly accurately transverse of the individual strands showed many different stages of nodal development. In the diagrammatic figures advantage has been taken of the opportunity to show two or three neighboring bundles in successive stages.

The increase in the amount of metaxylem first becomes apparent about 1200–1600 μ below the level of the actual departure of a trace. The additional tracheids are situated between the inner ends of the bands of metaxylem. There is no regularity in their order of development. Sometimes the first to lignify are those in contact with the tracheids of the lateral bands, but at other times the first additional tracheids to be formed lie in the middle of the parenchyma between the bands (fig. 1, stage 2). These tracheids are much smaller than the relatively large xylem elements situated near the inner ends of the lateral bands on which they abut. Generally the crossbar which is thus formed is at first only one tracheid deep, but it may attain locally a depth of two or three tracheids, even before the bar is complete. *Pari passu* with its formation, other relatively large tracheids develop in contact with the inner

ends and flanks of the lateral bands of metaxylem. This phase is represented in fig. 1, stage 3. During these and the two subsequent stages figured, certain partially torn elements of protoxylem may be found adhering to the carinal canal. Their presence is

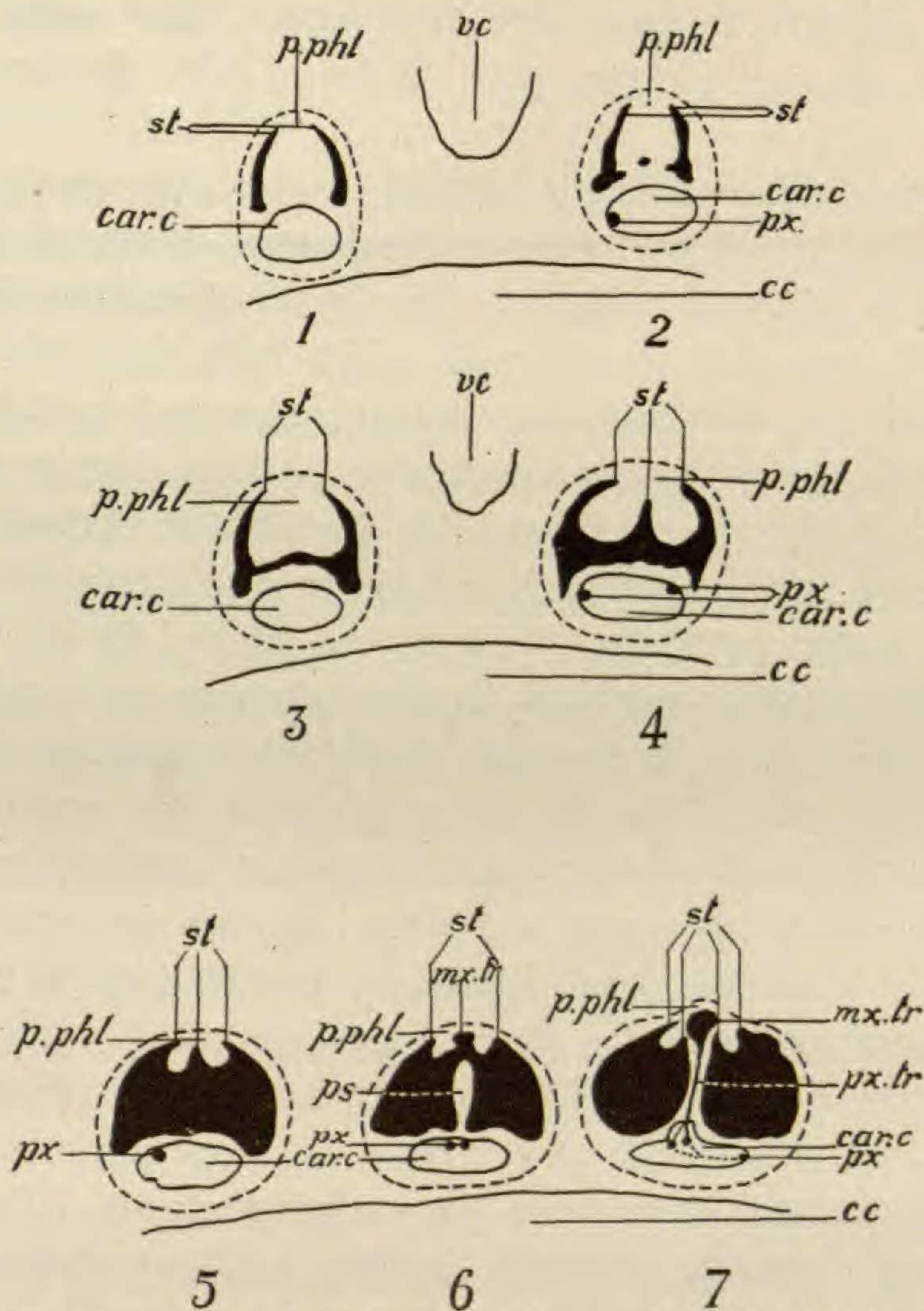


FIG. 1.—Stages 1-7, showing changes undergone by individual bundles in lower part of nodal region (xylem shown as black and endodermis as broken line): *cc*, central cavity of axis; *vc*, vallecular canal; *car.c*, carinal canal; *px*, protoxylem; *st*, small tracheids of metaxylem; *p.phl*, protophloem; *px.tr*, protoxylem of trace; *mx.tr*, metaxylem of trace; *ps*, parenchymatous sheath surrounding departing protoxylem of trace; $\times 120$.

very inconstant; they may be absent from many consecutive sections, nor is their frequency correlated with the increase in xylem which continues as the node is approached.

As we pass upward, the tracheids of the crossbar increase in number and size, especially in its median region, where the increase

leads to the formation of an outwardly projecting tooth (fig. 1, stage 4). The tracheids at the outer edge of the tooth are very small, and have exactly the same appearance as those at the outer edge of the parallel bands of metaxylem (*st* of the figures). Their thickening appears to be a fine reticulum. The more internal elements of the metaxylem, both those of the crossbar, which becomes radially deeper, and those at the thickened bases of the former internodal lateral bands, assume more and more the appearance of typical nodal tracheids of *Equisetum*; some of them are already much widened radially. The bundles increase in width, but are still separated by intervals wider than themselves. The carinal canals are still large, but become narrower radially. The median tooth of metaxylem eventually projects nearly as far as the ends of the lateral bands and the concavities between it, and then becomes much shallower, owing to the great increase in number of nodal tracheids. This is the phase shown in fig. 1, stage 5. The small concavities in the xylem on each side of the median tooth seem to be occupied chiefly by metaxphloem.

Soon after this stage has been reached, the smaller outer tracheids of the median tooth begin to project more and more, and the tooth becomes less acute in outline. At the same time two to four rows of tracheids, lying internally to these small projecting tracheids, are replaced by parenchymatous cells. In this way the inner part of the bundle is divided by a narrow parenchymatous gully, continuous with the two or three layers of parenchyma that separate the carinal canal from the nodal tracheids. The carinal canal is now markedly narrower radially, and usually contains at its outer edge, opposite the parenchymatous gully, the remains of two or three partially disorganized tracheids. This condition is represented diagrammatically in fig. 1, stage 6. Almost immediately after the formation of the parenchymatous gully a few of the partially disorganized tracheids of the protoxylem may be seen to bend outward from the carinal canal, which here bulges a little outward. These tracheids now, no longer disorganized, run through the parenchymatous gully and fuse with the small oval mass of tracheids that forms the upward continuation of the small tracheids at the apex of the median tooth of metaxylem. These latter

elements, constituting the metaxylem of the trace, are more numerous than the protoxylem elements that pass out into the leaf. The metaxylem of the trace detaches itself from the nodal tracheids of the bundle before the phloem of the trace is set free from that of the axis. The endodermis of the bundle is beginning to bulge out somewhat opposite the trace that is preparing to depart. During its passage through the bundle (fig. 1, stage 7) the protoxylem of the trace is very clearly distinguishable under the microscope from the metaxylem, because, in a transverse section of the axis, the protoxylem running out from the carinal canal is cut almost longitudinally, while the metaxylem, some of the elements of which are not much larger, is moving so slowly and steeply upward and outward that its tracheids are cut almost transversely. When the junction of the protoxylem with the metaxylem has been effected, the tracheids of the former bend sharply upward and pursue the same steeply oblique course as the elements of the metaxylem. At this level the protoxylem is again disorganized, so that the trace contains a small protoxylem canal. This at first lies at the inner edge of the wood, but soon becomes somewhat internal in position, so that the xylem of the trace becomes mesarch almost at once. Before the trace is set free its protoxylem has assumed an approximately central position.

When the protoxylem has passed through the parenchymatous gully, two to four rows of parenchymatous cells, resembling those occurring below and on the sides of the departing protoxylem, are found above the latter. Thus the protoxylem runs through the nodal tracheids surrounded by a sort of parenchymatous sheath.² Immediately above the cells of this sheath nodal tracheids again form, leaving, however, a parenchymatous notch opposite the point of departure of the xylem of the trace.

Concurrently with the appearance of these tracheids the carinal canal becomes much narrower radially, and frequently contains a certain number of somewhat torn tracheids. It is usually at this stage that the nodal xylem of adjacent bundles becomes confluent. This union may take place in two ways. Where (as was

² Such a parenchymatous gully has also been observed at the nodes of *E. palustre* and *E. hiemale*.

the case at the points of junction of by far the greater number of bundles) the stele of a branch was inserted on the axial stele, the bundles of the latter first became united by their outer ends. Here the nodal xylem unites to form a sort of arch (fig. 2, stage 8*b*). The curve of this arch constitutes the outer and lower half of the continuous hollow central cylinder of the branch at its oblique insertion on the axial stele.³ At a slightly higher level the more internal nodal xylem also becomes confluent, usually at a point about halfway between the periphery of the nodal xylem and its inner edge (fig. 3, stage 9). The tracheids at and near this junction

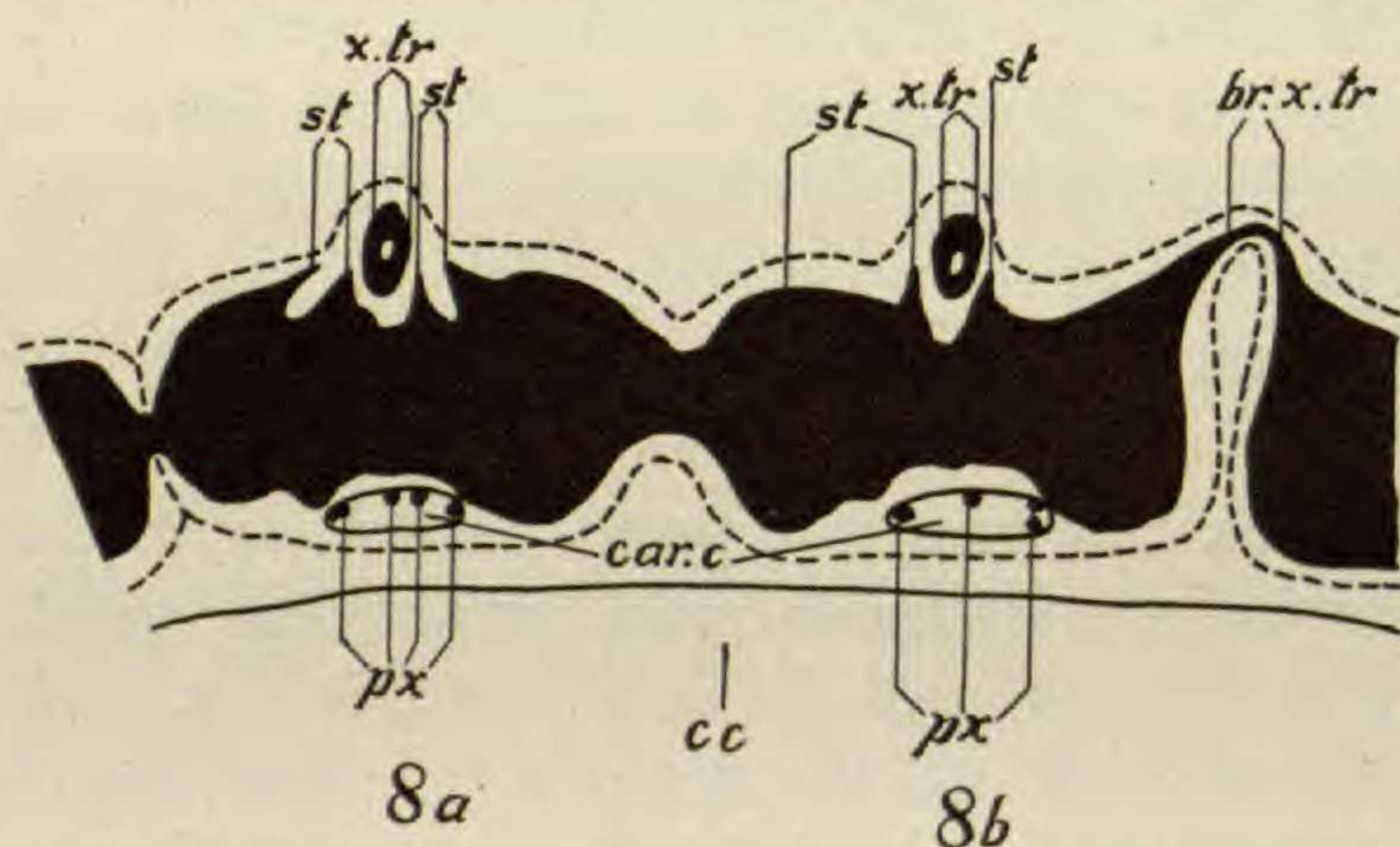


FIG. 2.—Stages 8*a* and *b*: *x.tr* xylem of trace; *br.x.tr*, xylem of branch trace; other lettering as in fig. 1; \times about 120.

mark the insertion of the inner higher portion of the continuous ring of wood of the branch. At this level, however, the lower outer edge of the siphonostele is no longer visible, so that no single section shows the complete siphonostele of the branch and the continuity of its "pith" with that of the stem. Where no branch is given off, the bundles become laterally united in their middle regions by a narrow neck of xylem, as shown on both sides of the bundle in fig. 2, stage 8*a*. This neck of xylem rapidly thickens. The special endodermes lie outside the nodal tracheids, and their fusion precedes the junction of the xylem of adjacent bundles.⁴ As we pass upward certain cells on the adjacent sides

³ For a fuller description of the insertion of the vascular system of the branch on that of the stem, see PFITZER (12, pp. 329-330, *pl. 20, figs. 19, 20, 23*).

⁴ A fuller account of the behavior of the special endodermes at the nodes will be found in PFITZER'S (12) description of their distribution at the nodes of *E. limosum* and *E. litorale*.

of two endodermal sheaths are replaced by single endodermal cells, common to both bundles. A little higher still these single endodermal cells are replaced by nodal tracheids, and the special endodermes by the common inner and outer endodermes typical of the vegetative nodes throughout *Equisetum*. When a branch is to be given off, the inner endodermis projects outward in a loop inside the arch of xylem representing the outer, lower insertion of the ramular siphonostele (fig. 2, stage 8*b*). In such a case the endodermal cells at the inner narrow end of the loop fuse before the junction of the nodal tracheids in this region. The endo-

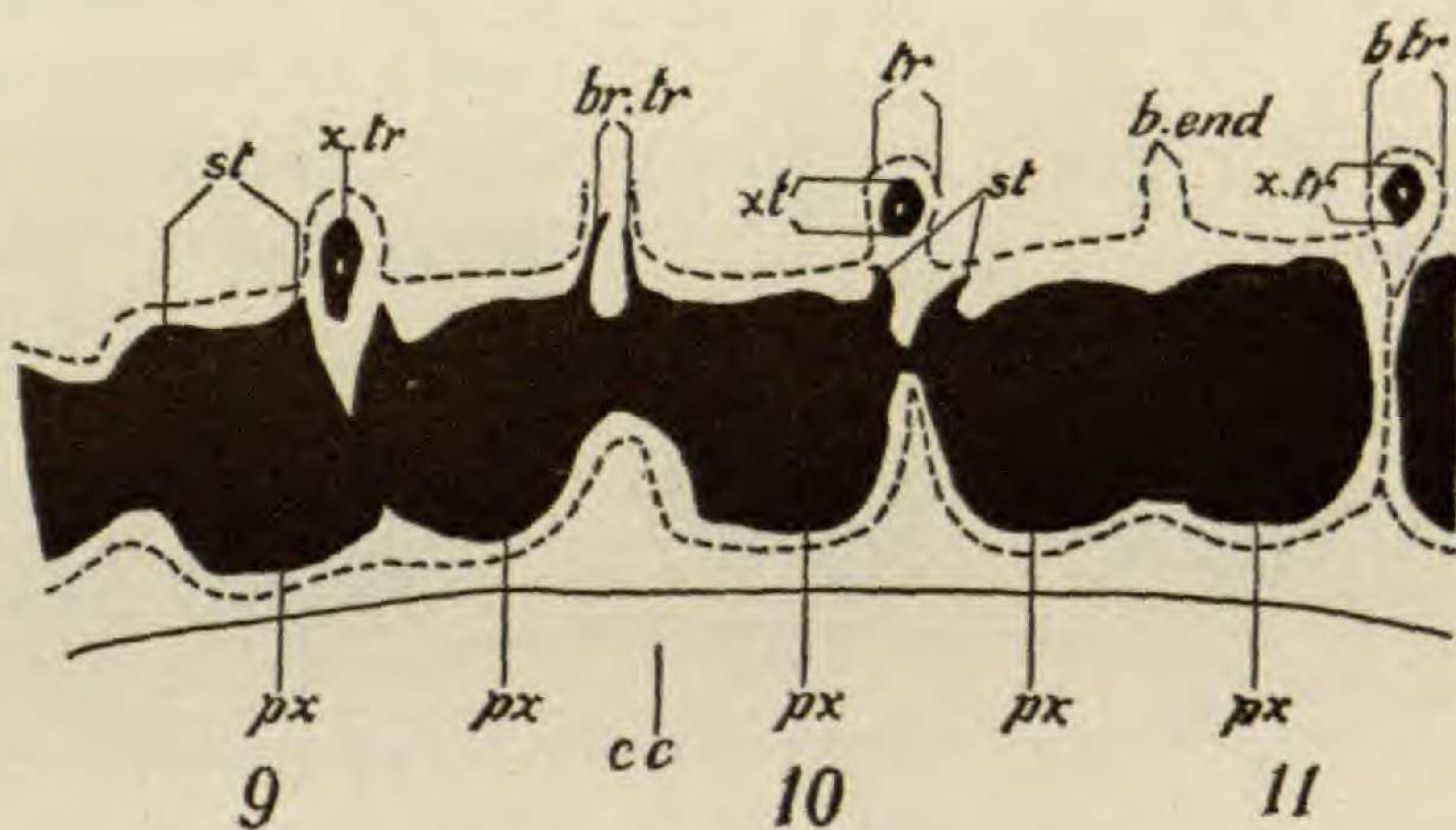


FIG. 3.—Stages 9-11; *br.x*, xylem of branch; *b.end*, endodermis of branch; other lettering as in figs. 1 and 2; \times about 120.

dermis of the branch is thus in continuity with the inner endodermis of the axis.

To return to the carinal canals, these dwindle rapidly after the nodal tracheids have spread over the parenchymatous sheath, and soon disappear. As most of the medianly situated protoxylem tracheids have departed into the leaf, this region consists chiefly of parenchyma, in which are sometimes found a few tracheids that die out as we pass upward. A few of the protoxylem elements, however, forming the upward continuation of the elements at the sides of the carinal canals, may be seen persisting as two little groups on each side of the parenchymatous sinus that replaces the carinal canal. At the same time the parenchymatous depression in the outer edge of the nodal wood, opposite the departing trace, deepens, as is shown in fig. 3, stages 9 and 10. Meanwhile the inner endodermis becomes involuted into the parenchymatous

sinus at the inner edge of the xylem (stage 10). This sinus lies opposite that in the outer edge of the metaxylem, and the latter is broken in this region by the deepening of both notches; through the break inner and outer endodermes become confluent. Soon the endodermis becomes double in the region of involution, and two separate bundles are reconstituted, alternating with those of the internode below. The inner part of the endodermis of the departing trace arises as a duplication of that part of the invaginated endodermis that constitutes the bundle sheath of the new bundles at the sides of the parenchymatous depression in the outer edge of the nodal xylem. It is at this moment that the

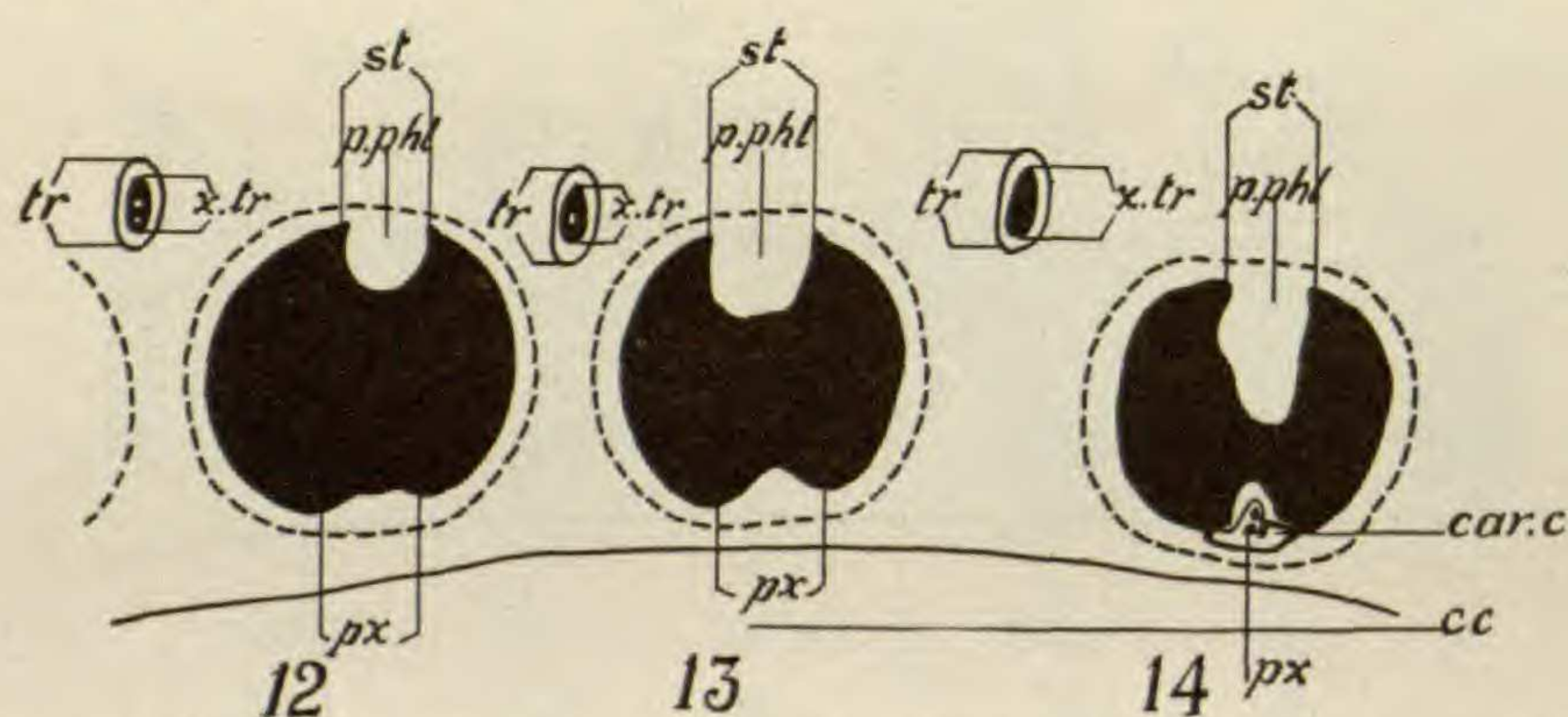


FIG. 4.—Stages 12-14: *en.tr*, endodermis of trace; other lettering as in preceding figures; \times about 120.

leaf trace finally becomes free from the axial tissues (fig. 3, stage 11).

As we pass upward above the departure of the traces, the nodal xylem of the newly constituted bundles diminishes in amount, and these become more and more widely separated (fig. 4, stages 12-14). Each of them carries with it two small groups of protoxylem, situated laterally at the inner limit of the nodal xylem. Traced downward, these groups are continuous with the protoxylem of two neighboring but independent bundles of the internode below. As the nodal xylem diminishes, the two groups of protoxylem adherent to it are brought nearer to one another, each becoming farther and farther removed from its sister strand, now included in a neighboring bundle. Just before, or when the new bundles become free from one another, a slight depression appears in the outer edge of the xylem, in the median region of each new

bundle (figs. 3 and 4, stages 11, 12). This deepens rather rapidly, and another shallower parenchymatous depression appears opposite it on the inner edge of the metaxylem, between the two groups of protoxylem (fig. 4, stages 12, 13). In this inner indentation a carinal canal now forms, or, in other words, the protoxylem strands arising from different bundles of the internode below approach one another, and, partly by an increase in their number, become united into a single group (fig. 4, stage 14). By this time the metaxylem has decreased considerably in amount, and forms a deeply lobed mass, the two lobes being separated by the deepening parenchymatous sinus in

the outer edge of the xylem. The lobes become less and less massive, and are soon only connected by a narrow crossbar. When this breaks, as it does a little higher up, the structure of the bun-

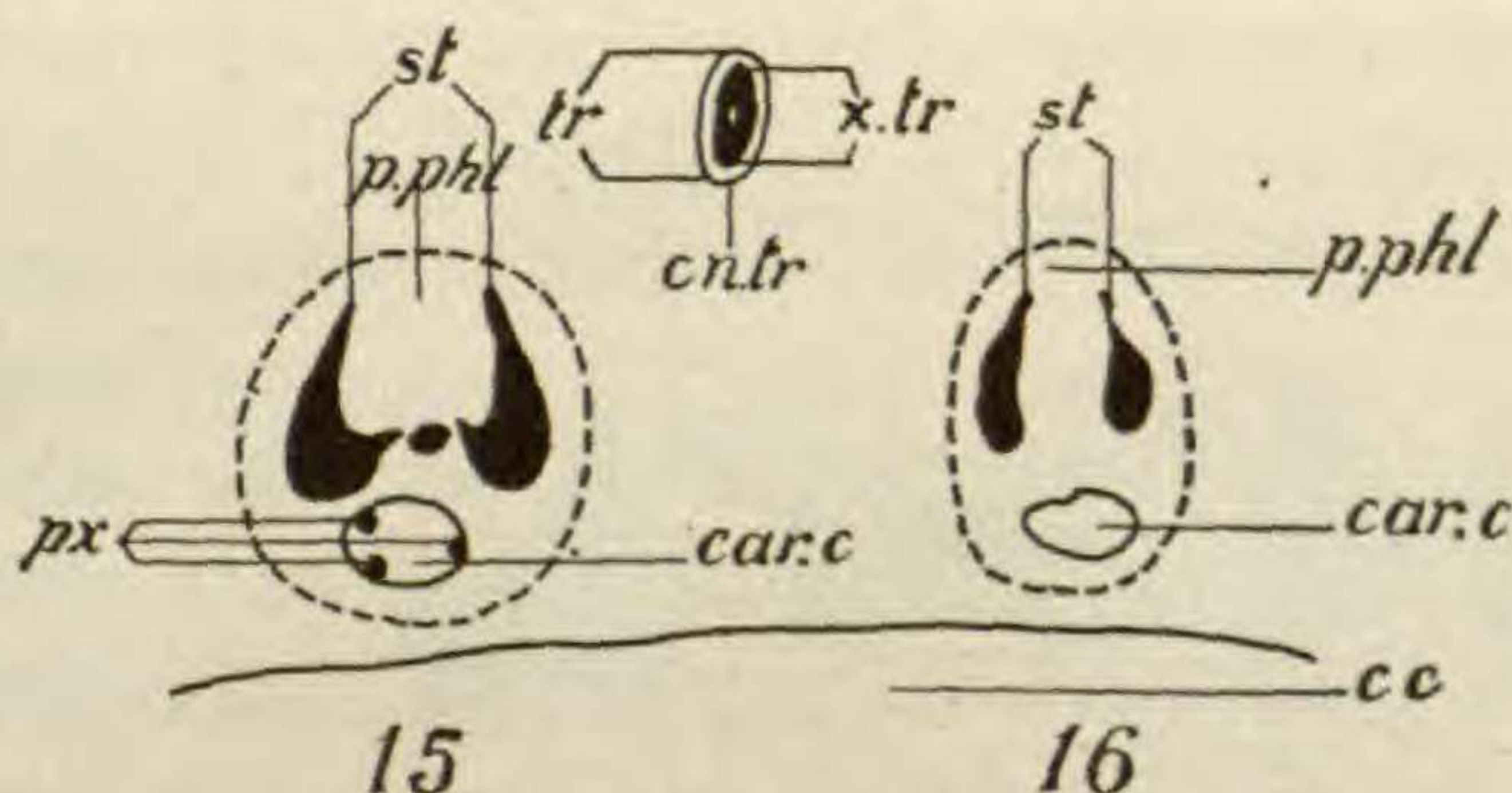


FIG. 5.—Stages 15 and 16; \times about 120

dle (fig. 5, stages 15, 16) vividly recalls stages 1 and 2 of fig. 1, although the metaxylem is as yet more extensive than in these. By a decrease in the number of tracheids, however, the bundles soon assume the internodal appearance shown in fig. 1, stage 1.

As in the cone-bearing stem of *E. limosum* described by the writer (3), so at this node of *E. giganteum* an inverted cone of relatively thick-walled cells, staining deeply with Bismarck brown, hangs down from the upper limit of the node for a little distance into the internode.

III. Nodes of smaller fertile branches

The upper nodes of the cone-bearing branches of *E. giganteum*, although resembling in essentials the node of the main stem previously described, were on a much smaller scale, and showed one or two points of difference. The branches at my disposal all possessed eleven ribs and bundles, and their steles were but little over a millimeter in diameter. There is no definite diaphragm, neither is there an inverted cone of persistent tissue hanging down

from the node; but the central cavity is much narrowed in the nodal region, and the stele itself decreases somewhat in width, as is well seen in longitudinal sections. Sometimes no branches are initiated at these nodes, but in other cases one or two branches may be initiated, even at the uppermost vegetative node. As we approach the node the lateral bands of metaxylem of each bundle become united, as in the bundles of the large node already described. The bundles, at the corresponding heights, have much the appearance of those shown in fig. 1, stages 1-3, except that by the time we reach stage 3 the carinal canal is being replaced by a group of slightly disorganized tracheids. The median tooth

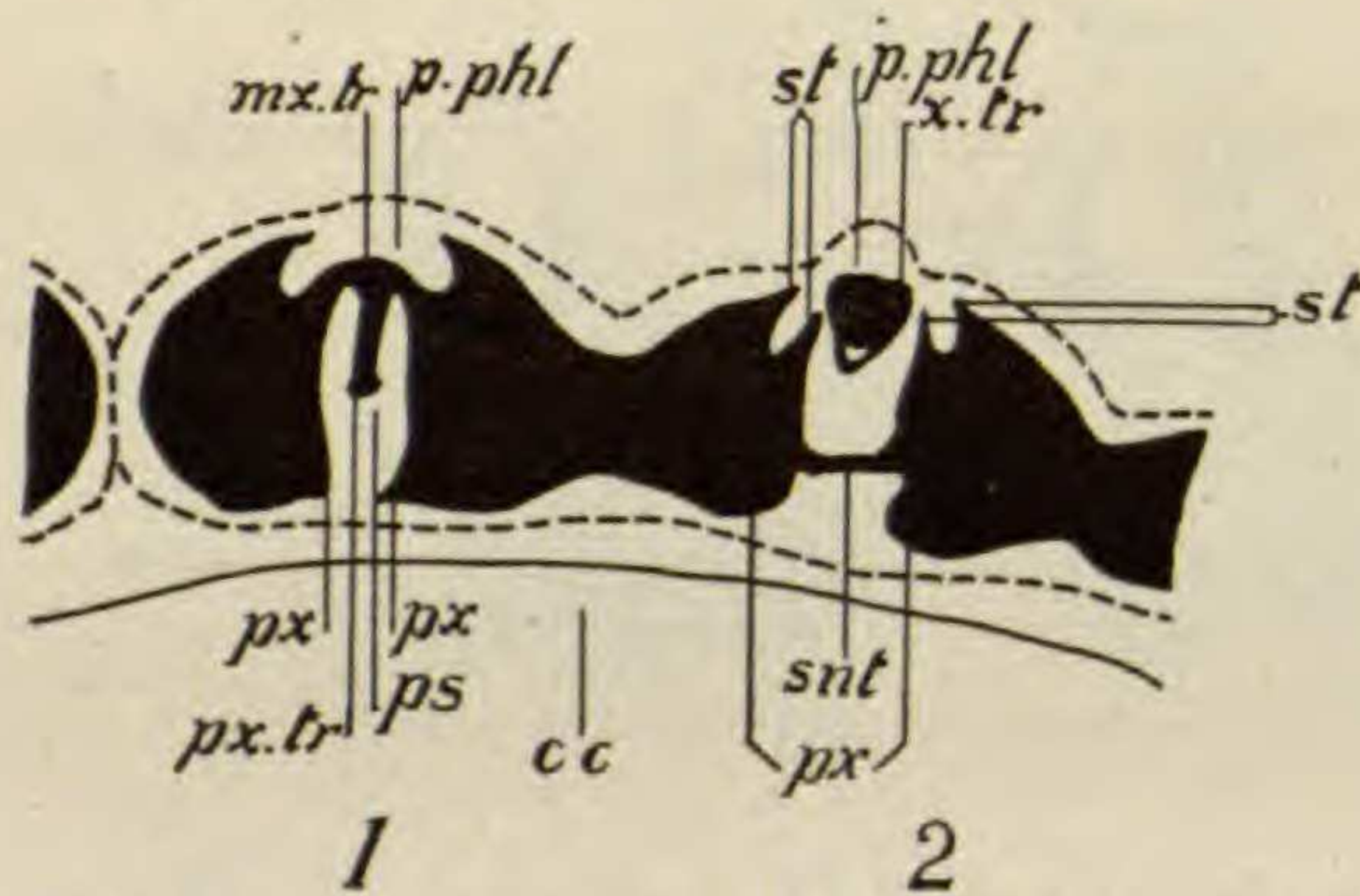


FIG. 6.—Stages 1 and 2; these stages show appearance of bundles of small cone-bearing branch of *E. giganteum* at levels of node corresponding to those shown for bundles of main axis in stages 7 and 8 of figs. 1 and 2; more highly magnified.

of xylem seen in stage 4 of fig. 1 is not developed, although in some of the bundles the crossbar is slightly thicker in its median region. As in the larger axis, the crossbar is separated from the carinal canal by two or three layers of parenchyma. Some of the protoxylem elements pass out very gradually, carrying with them such of the metaxylem elements of the crossbar as lie outside them.

The same parenchymatous sheath is formed for the passing out of the protoxylem. This sheath, which is relatively wide and conspicuous, is here directed obliquely upward, since the protoxylem, which lies in it, passes very slowly through the bundle. As there is here no median tooth of metaxylem, the metaxylem of the trace is more deeply situated in the bundle and nearer to the protoxylem, so that the protoxylem and metaxylem of the trace form, in most of their course through the bundle, a single, radially elongated mass of similarly oriented tracheids. This stage is shown in fig. 6, stage 1, a stage corresponding more or less with stage 7 of fig. 1. While passing through the bundle, the metaxylem of the trace remains in contact at its outer end with the nodal xylem of the

bundle. When the xylem of the trace detaches itself from the axial wood, it forms an isosceles triangle, sometimes containing one or two parenchymatous cells. At the inwardly directed apex of the triangle lies the protoxylem. In most cases at least, a few of the tracheids at the sides of the wide, outwardly directed base of the triangle are derived from the peripheral nodal xylem of the bundle. By the time the trace has become free and provided with a separate endodermis, its xylem has become or is becoming slightly mesarch. As the trace moves out, a bar of metaxylem, usually only one cell in depth, forms across the inner end of the parenchymatous sheath (fig. 6, stage 3). These tracheids very soon die out in passing upward. Although few in number, they seem to represent the much greater extent of median supranodal xylem of stages 8a and 8b of fig. 2.

It should be pointed out that, as in the node of the larger axis, some elements of the protoxylem, although here only a very few, persist on either side of those that depart to the trace. Each of the reconstituted bundles possesses two groups, derived respectively from the two bundles alternating with it in the internode below. Owing to the smaller size of the bundles, these two groups of protoxylem are nearer to one another than in the bundles of the main axis. They soon unite, forming with additional elements the protoxylem strands of the new internode. These groups of protoxylem traversing the node are very small and inconspicuous, and might easily be overlooked or taken for the narrow ends of nodal tracheids. It is possible that sometimes one of them may die out and not be continued in the internode above, but this could not be satisfactorily determined from the material.

IV. Branches initiated on main stem

One point in connection with the numerous branches initiated on the large young axis of *E. giganteum* deserves mention. None of these branches, the cells of which were active in process of division, had yet broken through the tissues of the leaf sheath of the parent axis. As they alternate with the teeth of this sheath, their median line coincides with the commissural furrow, or line of congenital fusion of two leaves. This furrow projects markedly

inward, causing a slight depression in the ochreola or lowest sheath of the branch. The ochreola, which is much better developed on the side away from the parent axis, possesses five teeth, forming in the lower part of the sheath five inconspicuous blunt ribs. The two which lie most externally, right and left of the slight median depression, are by far the most developed. Even in this early stage, in most cases at least, both possess a small vascular bundle containing two or three small tracheids. Cases have previously been recorded and figured in which the ochreola is penetrated by one vascular bundle (8, 11).

V. Young internode of main stem

The base of the leaf sheath is concrescent with the axis. At the level at which the former becomes free in the large young axis the tissues of the main stem have the appearance of being very young. The cells mostly have large nuclei and are rich in contents; no metaxylem has been differentiated, nor is the bundle sheath recognizable; most of the protoxylem still persists. The cortical cells below the ribs of the stem, which later develop as sclerenchymatous fibers, still have unthickened walls. As we pass upward in the internode the tissues gradually assume a more mature appearance. This should be expected, since it is known that the metaxylem of an internode undergoes lignification from above downward (1). In this lower end of a young internode, therefore, we have an anatomically incompletely differentiated portion of the axis of *E. giganteum*, the absence of which prevented GWYNNE-VAUGHAN from definitely establishing the direction of lignification of the lateral metaxylem in this species. He suspected that the direction of lignification in *Equisetum* generally was centripetal in the lateral strands of metaxylem. He held that this was indicated by the constantly smaller size of the peripheral tracheids in *E. giganteum*, the species in which the lateral metaxylem is most abundantly developed.

Near the base of the young internode, at the point at which the leaf sheath detaches itself from the axis, no metaxylem had been differentiated. As we pass upward one or two laterally situated tracheids soon make their appearance, but in most of the bundles it

is only about 1 mm. higher up that the lateral metaxylem consists of a number of tracheids more or less equivalent to the number found in a mature internodal bundle. The serial sections were 14 μ in thickness, and thirty-two bundles of a section often showed different stages of the differentiation of the laterally situated tracheids. It was possible, therefore, to examine very numerous examples of incompletely differentiated metaxylem. Some irregularities were observed, but no doubt was possible that in the very great majority of cases the small outer tracheids are the first to become lignified. Thus in this species, as GWYNNE-VAUGHAN suspected, the metaxylem develops centripetally. Not infrequently, after the lignification of two or three small elements at the periphery of the wood, the next element to be lignified is larger and much more deeply seated. Commonly, however, the lignification proceeds more or less regularly from without inward.

VI. General considerations

Conflicting statements have appeared as to whether the protoxylem of *Equisetum* persisted through the nodes or disappeared at this level. JEFFREY (9), in 1899, wrote that in the nodal region the vascular tissue was massive and entirely devoid of typical protoxylem elements, and in comparing the node of *Equisetum* with the description given by WILLIAMSON and SCOTT of that of a Calamite, he states that in the recent genus the protoxylem comes to an end below the node, and that it is absent from the inside of the nodal wood. LUDWIGS (10) also appears to regard the protoxylem as disappearing at the nodes. He writes as follows:

At the node the protoxylem passes out as a bundle into the leaf, the groups of metaxylem approach one another and, uniting with the xylem of the next internode, completely fill up the carinal canal. In the position of the latter we find a large number of vessels with reticulately thickened walls, whereas the elements of the protoxylem show annular thickenings.

More recently Miss BARRATT (1) has asserted that the protoxylem does not traverse the node. In 1901, however, GWYNNE-VAUGHAN described the forking of the leaf trace protoxylem of *Equisetum* at the node and the fusion of each fork with the adjacent fork of protoxylem of a neighboring bundle. In 1908 BOWER (2)

adopted GWYNNE-VAUGHAN'S conclusions as to the basis of his description of the course of the bundles of *Equisetum*, illustrating this course by means of a hitherto unpublished diagram constructed by the latter.⁵ QUÉVA (14) in his very careful researches

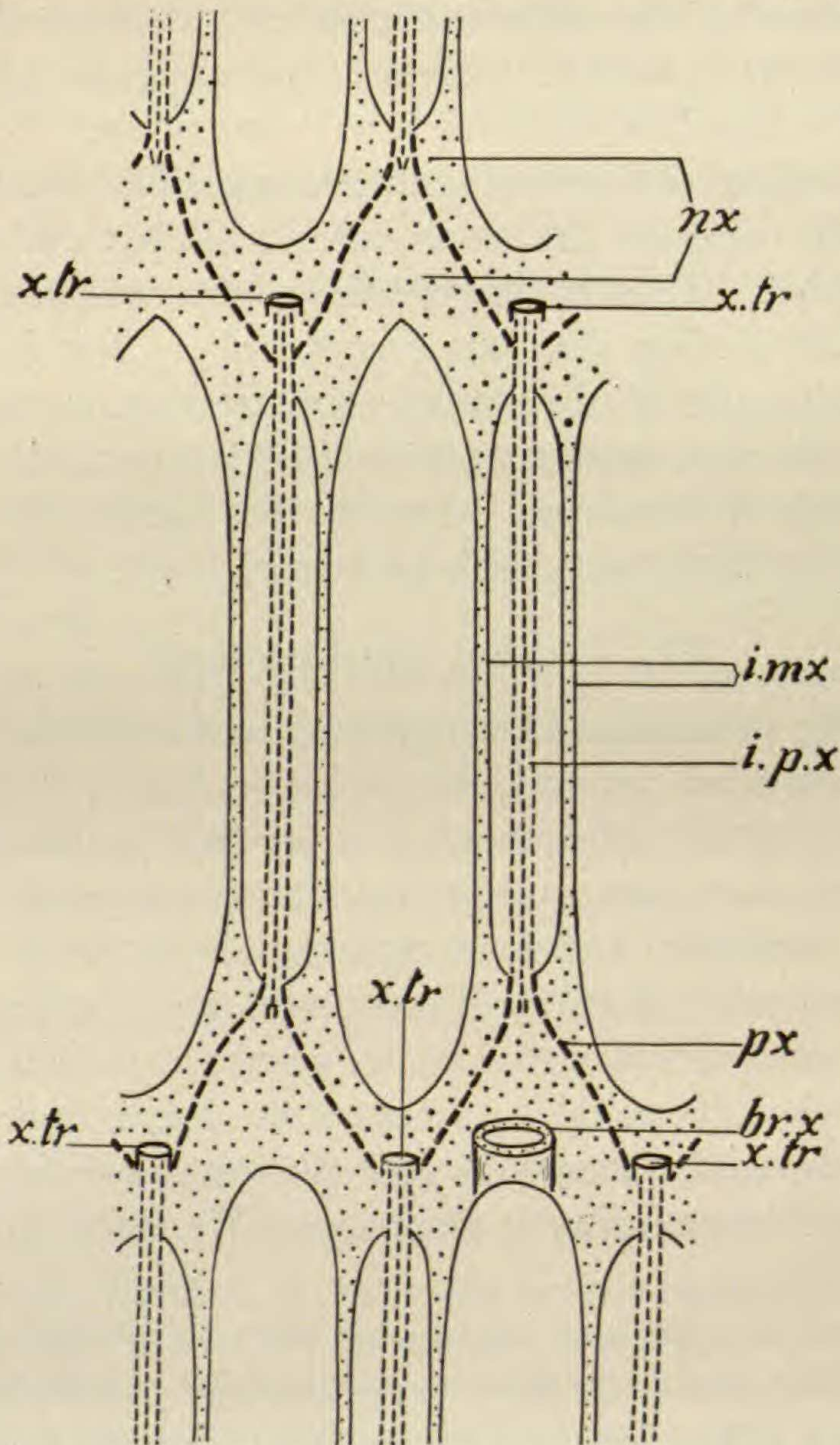


FIG. 7.—Diagram showing distribution of xylem of *E. giganteum* (protoxylem indicated by broken vertical lines, metaxylem by dotted surface): *x.tr*, xylem of trace; *br.x*, xylem of branch; *px*, protoxylem; *i.p.x*, protoxylem of internode; *nx*, nodal xylem; *i.mx*, internodal metaxylem.

⁵ This diagram is in disagreement with the comparable fig. 7 of the present paper in that in it the lateral internodal strands are made to persist through the node. As GWYNNE-VAUGHAN'S diagram was constructed only to show the course of the strands of the internodal bundle at the node, the distribution of the nodal xylem is not indicated in it.

gave no written description of the course of the protoxylem above the departure of the xylem of the trace. In describing the nodal xylem of *E. maximum*, however, he states that at the inner edge of each of the masses of nodal wood some protoxylem elements (his trachées) are always found. These axial protoxylem elements are shown before the lignification of the nodal tracheids in his figs. 16 and 17, and after the differentiation of the nodal wood in his figs. 18 and 19 (all of *E. maximum*). Moreover, his fig. 22 of *E. litorale*, in which two traces⁶ may be seen, already some way out in the cortex, shows very clearly the protoxylem persisting from the bundles of the internode below. In this figure the protoxylem of each of these bundles has been divided into two groups of tracheids, and these sister groups have already diverged somewhat from one another.⁷ EAMES (6) also regards the protoxylem as persistent, for in discussing the nodal, or as he calls it, the supranodal wood, he states: "Certainly its innermost elements are protoxylem, many radial sections show this condition clearly." Later, in summarizing the nodal structure of *Equisetum*, he states: "The carinal canal becomes discontinuous as it approaches the node. The protoxylem occupying that space enlarges, extending radially, then passes upward and forms the innermost tracheids of the supranodal wood." From these statements it would seem that EAMES holds that the protoxylem persists through the node, although hardly as distinct strands; he seems rather to regard the inner elements of nodal xylem generally as protoxylem.

The description of the nodal region of *E. giganteum* here given entirely confirms, so far as the course of the protoxylem is concerned, GWYNNE-VAUGHAN'S account. This might have been expected, as this author alone appears to have worked on the nodes of *E. giganteum*. It is, however, in agreement with QUÉVA'S less complete account of the protoxylem at the node, and in particular with his figures of *E. maximum* and *E. litorale*.

⁶ Only a portion of the trace on the left is included in QUÉVA'S figure.

⁷ In view of QUÉVA'S figures just mentioned, and of his allusion to the presence of protoxylem at the inner edge of the nodal wood, I cannot agree with Miss BARRATT'S statement that he had noted that the xylem of each internode develops quite independently, only linking up subsequently by the development of the nodal tracheids.

Examination of serial sections through nodes of a cone-bearing branch of *E. palustre* and of a fertile stem of *E. sylvaticum* showed that the continuity of the protoxylem strands through the node, their forkings and fusions, could very well be followed in these species. In both the course of the protoxylem at the node corresponds with that of the protoxylem in *E. giganteum*. The distinction between nodal wood and protoxylem is very clear, although the innermost nodal tracheids are relatively small. In both species the persistent protoxylem is sometimes locally separated from the inner edge of the nodal wood by a parenchymatous cell or two. In *E. sylvaticum* the persistent tracheids of protoxylem are relatively numerous, and some of the medianly situated ones may persist for a little distance above the departure of the tracheids of the trace. In a young node of a fertile stem of *E. arvense* that had not yet appeared above ground it was possible to observe the persistence of the protoxylem and indications of its forkings and fusions at the node. The phenomena, however, were not so clear.

Serial sections through a vegetative node of the cone-bearing branch of *E. debile* showed that in this species also two small groups of protoxylem, consisting of a few tracheids only, persisted after the departure of the trace. On the breaking up of the nodal xylem these two small strands entered separate but adjacent bundles. Each of the newly constituted bundles, therefore, possessed two of these small strands of protoxylem. These, however, did not always fuse to form the protoxylem strand of the internode. Frequently one, sometimes both, seemed to die out. In the latter case the protoxylem of the upper internode was unconnected (except by nodal tracheids) with that of the lower internode. In other cases a few elements of one or both branches of protoxylem linked up the protoxylem of one internode with that of the other.

In the specimens of *E. hiemale* of which I have examined serial sections, the protoxylem disappears at the nodes; in other words, the whole of it passes out into the trace. In this species the internodal bundles are relatively far apart, and the bundles of successive internodes are formed by the oblique course and fusion of adjacent halves of neighboring bundles. During the oblique course of the halves it is easy to see that all the tracheids com-

posing them are reticulately thickened. In nodes of the fertile stem of *E. maximum* I was able to trace the forking of the persistent protoxylem, the divergence of the forks, and their passage into separate though neighboring bundles. Each of the newly constituted bundles thus contained two small groups of protoxylem, but in no case could a connection between these forks and the protoxylem of the internode above be observed; they seemed always to die out.

As we are dealing in *Equisetum* with plants showing a reduced vascular system, it is probable that the dying out of part or all of the protoxylem of one internode without coming into connection with the protoxylem of the next is a derivative character, and that the course of the protoxylem described for *E. giganteum* is primitive within the genus. In this connection it may be pointed out that in the fertile stem of *E. maximum*, although the bundles are of much the same width as those of the large young axis of *E. giganteum* described in this paper, the height and the radial extent of the nodal wood of the latter, even in its young condition, were nearly twice as great as the height and depth of the nodal wood at the nodes of the fertile stems of *E. maximum* studied. Moreover, it has been shown (4) that the cone of *E. maximum* has a much reduced vascular system.

It is possible that at the nodes of the sterile stems of *E. arvense* and *E. maximum* none of the protoxylem, at least in typical cases, persists above the departure of the tracheids of the trace. This appears to be the view of JEFFREY and Miss BARRATT. On the other hand, QUÉVA's figures seem to show that sometimes at least the protoxylem persists, at any rate for some distance above the departure of the tracheids to the trace. Such protoxylem as persists at the node is small in amount and often inconspicuous, so that in many cases it may well have passed unnoticed. When, however, as in *E. hiemale*, the protoxylem disappears completely at the level of the departure of the tracheids of the trace, this would seem to be due to a further reduction along the lines exemplified at the nodes of the fertile axes of *E. debile* and *E. maximum*.

Passing from the consideration of the protoxylem to that of the metaxylem, we again meet with a conflict of evidence. In 1890

POIRAULT (13) asserted that the metaxylem developed centripetally, and eleven years later GWYNNE-VAUGHAN was led by his study of the vascular system of *E. giganteum* to adopt a similar view, although in the absence of an incompletely differentiated portion of the axis of this species he considered the centripetal development of the xylem as not established. As has been pointed out, a study of the young internode of *E. giganteum* confirms GWYNNE-VAUGHAN'S opinion, and it seems clear that in this species the direction of lignification, although subject to slight irregularities, is from without inward. On the other hand, QUÉVA in 1907 showed clearly that in *E. maximum* the lateral metaxylem of the internode was differentiated centrifugally. EAMES claimed that although there is a good deal of irregularity in the direction of its lignification, the internodal metaxylem was differentiated centrifugally in the majority of the bundles of *E. maximum*, *E. arvense*, and *E. hiemale*. This has recently been confirmed by Miss BARRATT for the first two species. Serial sections of the internodes of young cone-bearing branches of *E. arvense*, *E. limosum*, and *E. debile*, in which the lateral metaxylem was incompletely differentiated, were examined for comparison with the young internode of *E. giganteum*. In all of them the differentiation of the metaxylem, although subject to occasional irregularities, as EAMES has pointed out, was in the great majority of cases clearly centrifugal.

It seems difficult to doubt the essential homology of the characteristic lateral groups of metaxylem throughout the genus *Equisetum*. The question, therefore, arises whether the primitive order of development of the metaxylem was centripetal or centrifugal. It is undeniable that the metaxylem, both nodal and internodal, is better developed in *E. giganteum* than in any of the other species the anatomy of which has been studied. Moreover, in a genus showing an obviously reduced stelar structure the species with the largest amount of xylem would naturally seem to be the most primitive. On the other hand, *E. giganteum* is exceptional, so far as we know unique, in the centripetal development of its metaxylem. It is even possible that such centripetal development might be confined to the base of the internodes, although on general grounds and in view of the constantly much

smaller size of the peripheral tracheids this does not seem to be likely. Perhaps the strongest argument against the primitiveness of the centripetal development of the lateral metaxylem lies in the position of this tissue outside the endarch protoxylem, which makes it difficult to regard it as a vestige of the central centripetal xylem of a protostele. For the present, therefore, it seems premature to draw any definite conclusions from the exarchy of the internodal metaxylem in the axis of *E. giganteum*.

GWYNNE-VAUGHAN also stated that in *E. hiemale*, and better still in *E. giganteum*, the lateral internodal strands of xylem could be traced, after joining on to the nodal wood, as externally projecting ridges into the internode above.⁸ He claimed that these lateral strands diverged while passing through the node, so that in the internode above they were situated on adjacent sides of separate bundles; that at the next node these strands again approached one another, and that in the internode above this node the strands were again included in the same bundle. In fact, according to this author, the course of the metaxylem strands at the node is exactly that described in this paper as characteristic of the protoxylem of *E. giganteum* in this region. In this species the lateral strands of metaxylem are composed of numerous elements, and if they persisted through the node they would be very conspicuous. From the serial sections of the nodes at my disposal, however, it was clear that the identity of the lateral strands was completely lost in the relatively large tracts of nodal xylem. As we approach the nodes the tracheids of the lateral strands gradually assume the appearance of typical nodal tracheids. QUÉVA has noted this gradual passing of the lateral metaxylem into the nodal wood in *E. maximum*. In this species, in which according to him the lateral metaxylem consists of tracheids with spiral or annular thickening, elements with a type of ornamentation intermediate between these and reticulate thickenings occur, he says, below the nodal wood and in continuity with the internodal metaxylem. Elements with this internodal type of thickening

⁸ I regret that in a recent paper (5) I alluded to GWYNNE-VAUGHAN'S claim of the persistence of the lateral strands "inside and over" the ring of reticulate tracheids. The passage should read "outside and over the ring of reticulate tracheids."

of course do not occur below the node of *E. giganteum*, since, as GWYNNE-VAUGHAN himself has shown, the internodal metaxylem, as well as the nodal xylem of this species, consists of reticulately thickened elements. Fig. 7 shows diagrammatically the distribution of the xylem at the nodes and internodes of *E. giganteum*. The spirally thickened protoxylem is there shown by broken vertical lines, while the reticulately thickened tracheids, nodal wood, and internodal lateral strands alike are shown by a dotted surface. For the sake of convenience the internodes have been drawn as much shorter than they would be in a mature specimen.

In *E. hiemale* the lateral strands are smaller than in *E. giganteum*, but it seemed clear from serial sections that they too completely lose their identity in the nodal wood. Indeed, this occurs relatively quickly, for the crossbar of the tracheids, which as we approach the node forms a bridge between the two lateral strands (fig. 1, stage 3 of *E. giganteum*), is here usually two, three, or more cells in depth, and therefore nearly as deep as the lateral strands. Thus the latter hardly project at all outward, and are early merged in an almost straight, oblong band of metaxylem lying outside and parallel to the radially narrow carinal canal. GWYNNE-VAUGHAN also claimed that in *E. maximum* no metaxylem departed from the axis to the leaf trace, although he made no statement on this point for *E. giganteum*. EAMES, however, claims that the metaxylem unquestionably takes part in the formation of the leaf trace, and figures such a case for *E. hiemale*, in which species the metaxylem is well developed. In nodes from three stems of *E. hiemale* examined the departing protoxylem carried with it metaxylem tracheids from the periphery of the bundle. At least in my specimens, however, these were less numerous than in *E. giganteum*, and died out before the trace with its endodermis was completely free from the axial bundle. In serial sections of nodes from two fertile stems of *E. maximum* and from a fertile stem of *E. sylvaticum* examined the metaxylem did not, in most of the bundles, contribute to the formation of the leaf trace, although occasionally in *E. maximum* and not infrequently in *E. sylvaticum* two or three reticulate tracheids, at the level of the departure of the trace, did bend out into the cortex, where, however, they seemed to die out.

Summary

1. The direction of differentiation of the metaxylem in the internode of *E. giganteum* is subject to slight irregularities, but is mainly centripetal. The outer elements are the smallest, and the tracheids, usually about 10-15 in number, become wider in passing inward.

2. These lateral, internodal strands of xylem join on to the nodal wood, at which level they lose their identity. There is no indication in *E. giganteum* of their persisting as strands external to the nodal wood.

3. The protoxylem is continuous through the node of *E. giganteum*. By the departure of the medianly situated tracheids to the trace the protoxylem is divided into two small groups of elements. These two groups diverge and enter neighboring but separate bundles of the internode above. Each of these small strands of protoxylem, diverging still farther from its sister strand, now situated in another bundle, fuses in the median region of the new bundle with an equivalent strand of protoxylem derived from the adjacent bundle of the internode below. The fusion is effected partly by a sudden increase in number of the protoxylem elements.

4. The nodal wood of *E. giganteum* attains a considerable height and radial depth. Wide, reticulate, typically nodal tracheids appear considerably below and persist for some distance above the departure of the traces.

5. The protoxylem elements of *E. giganteum* are situated at the interior of the xylem, and pass through the inner part of the metaxylem of the bundle in a kind of parenchymatous sheath, two to four cells in thickness. A considerable number of small metaxylem tracheids pass out into the trace, the metaxylem in the trace being usually greater in amount than the protoxylem.

6. In young branches of *E. giganteum* which had not yet broken through the leaf sheath of the parent axis, two of the ribs of the ochreola contained a small vascular bundle.

7. It is concluded that the continuity of the protoxylem of the internodes through the nodes, which, although not characteristic of all species, is not confined to *E. giganteum*, is a primitive character within the genus. The question as to whether the lateral

metaxylem of the genus was primitively centripetal, as in *E. giganteum*, or primitively centrifugal, as in the other species the detailed anatomy of which is known to us, is left open.

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